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1. AGENCY USE ONLY (Leave blank)		2. REPORT DATE May 2, 1996	3. REPORT TYPE AND DATES COVERED Final
4. TITLE AND SUBTITLE Delayed recovery of seagrass beds along navigable waterways: interaction between disturbance and nuisance algae			5. FUNDING NUMBERS DAAH04-93-2-0020
6. AUTHOR(S) Jeff G. Holmquist			
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) University of Puerto Rico - Mayagüez P.O. Box 5000 Mayagüez, PR 00681-5000			8. PERFORMING ORGANIZATION REPORT NUMBER
9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES) U.S. Army Research Office P.O. Box 12211 Research Triangle Park, NC 27709-2211			10. SPONSORING / MONITORING AGENCY REPORT NUMBER ARO 32454.1-GS-ISP
11. SUPPLEMENTARY NOTES The views, opinions and/or findings contained in this report are those of the author(s) and should not be construed as an official Department of the Army position, policy or decision, unless so designated by other documentation.			
12a. DISTRIBUTION / AVAILABILITY STATEMENT Approved for public release; distribution unlimited.		12 b. DISTRIBUTION CODE 19960522 062	
13. ABSTRACT (Maximum 200 words) In coastal systems, patches of seagrass are frequently destroyed by propeller scarring and anchor damage near waterways, resulting in denuded "blowouts". Persistence of blowouts is a poorly understood phenomenon, and I proposed that 1) benthic "drift" algae (marine analogs of terrestrial tumbleweeds) settle in blowouts and protract recovery of seagrass by shading the affected patches, and 2) that algal masses may be more easily trapped in small blowouts than in large blowouts. I tested this hypothesis with a series of field manipulations. Algal cover was much higher on disturbed plots than on controls, and there was also greater algal accumulation associated with small disturbances than with larger gaps. Algal accumulation slowed recovery of seagrasses as gauged by seagrass cover and density of seagrass shoots but caused little effect on recovery rates for standing crop, leaf area index, or canopy height. A greater intensity of disturbance fell upon the smaller plots, but recovery on these gaps was equal to or greater than exhibited by the large gaps, probably due to the small amount of vegetative recovery required to seal small gaps. There is thus evidence that large ambient populations of nuisance macroalgae can slow recovery of anthropogenously-disturbed vegetation along waterways.			
14. SUBJECT TERMS seagrasses, drift algae, macroalgae, disturbance, <u>Thalassia</u> , blowout, <u>Dictyota</u> , manipulation, gaps, patches, recovery, standing crop, leaf area index, canopy height			15. NUMBER OF PAGES 45
			16. PRICE CODE
17. SECURITY CLASSIFICATION OR REPORT UNCLASSIFIED	18. SECURITY CLASSIFICATION OF THIS PAGE UNCLASSIFIED	19. SECURITY CLASSIFICATION OF ABSTRACT UNCLASSIFIED	20. LIMITATION OF ABSTRACT UL

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**Delayed recovery of seagrass beds along navigable waterways:
interaction between disturbance and nuisance algae**

Final Progress Report

Submitted by: Jeff G. Holmquist

2 May 1996

Submitted to: U.S. Army Research Office

cooperative agreement DAAH04-93-2-0020

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Table of Contents

List of tables.....	3
List of illustrations.....	4
Statement of problem studied.....	5
Introduction.....	5
Objectives.....	11
Study Site and Methods.....	11
Summary of most important results.....	14
Data.....	14
Significance.....	15
List of participating scientific personnel.....	18
Bibliography.....	19
Tables.....	28
Figure legends.....	34
Figures.....	36

List of Tables

Table 1. Percent seagrass cover as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

Table 2. *Thalassia* shoots/m² as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

Table 3. Standing crop as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

Table 4. Leaf area index as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

Table 5. Canopy height as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

Table 6. Percent algal cover as a function of algal access and time since disturbance: results of multiple t-tests for treatment effects at selected intervals since disturbance.

List of Illustrations

Figure 1. Experimental design and layout of field manipulation.

Figure 2. Percent seagrass cover as a function of algal access and time since disturbance.

Figure 3. *Thalassia* shoots/m² as a function of algal access and time since disturbance.

Figure 4. Standing crop (grams dry mass/m²) as a function of algal access and time since disturbance.

Figure 5. Leaf area index (m²/m²) as a function of algal access and time since disturbance.

Figure 6. Canopy height (mm) as a function of algal access and time since disturbance.

Figure 7. Percent algal cover as a function of algal access and time since disturbance.

Figure 8. Percent algal cover as a function of size of initial gap size and time since disturbance.

Figure 9. Percent seagrass cover as a function of size of initial gap size and time since disturbance.

Figure 10. *Thalassia* shoots/m² as a function of size of initial gap size and time since disturbance.

Statement of problem studied

Introduction

Seagrasses are crucial to the continued functioning of coastal ecosystems and offset human disturbance in a variety of ways. These underwater meadows function as sediment traps (Ward et al., 1984) and damp wave action (Fonseca and Calahan, 1992) and current scour (Fonseca et al., 1982; 1983; Harlin et al., 1982; Bulthuis et al., 1984; Fonseca and Fisher, 1986; Fonseca, 1989). Grassbeds have proximate economic value, because, as Fonseca and Calahan (1992) suggest, the plants should reduce boat wake energy along intracoastal waterways and mitigate shoreline and subtidal erosion; seagrasses can be a cost-efficient alternative to jetties and other expensive stabilization methods (Fonseca and Fisher, 1986). Seagrass beds, like other types of submerged aquatic vegetation (SAV), support a remarkably high species richness and abundance of fauna (e.g., Orth et al., 1984; Holmquist et al., 1989a; Sogard et al., 1989) and provide an important nursery habitat for food and game fishes (Zieman, 1982; Livingston, 1984; Hettler, 1989). High abundances of both commercially-important species and smaller forage organisms in seagrass systems are the result of the predation refugium provided by the complex canopy of grass blades (Lewis and Stoner, 1983; Leber, 1985; Wilson et al., 1990). Seagrasses exhibit extremely high primary and secondary production which together form the underpinnings of other coastal systems external to the seagrass meadows (Zieman, 1982).

A variety of human activities can directly and negatively impact seagrasses. Much of this impact is associated with dredging of channels and other waterway impacts in shallow coastal systems (Zieman, 1982; Eleuterius, 1987; Livingston, 1987). Initial destruction by dredging is often

considerable (Taylor and Saloman, 1968; Godcharles, 1971; Zieman, 1975), and increased turbidity and sedimentation stemming from unvegetated channel bottoms and spoil banks can impose long-term stress on seagrass systems (Odum, 1963; Van Eepoel and Grigg, 1970; Grigg et al., 1971; Pérès, 1984; Shepherd et al., 1989). These channels provide access to shallow waters for relatively large vessels, and navigational errors result in propeller scars (Wanless, 1969; Zieman, 1976; González-Liboy, 1979; Delgado Hyland, 1991) and resuspension of sediments by propeller and wake scour (pers. obs.). In addition, vessels prefer to anchor in grassbeds, because anchors grip the rhizome layer more effectively than moorings in nearby unvegetated sediment; damage from these anchor scars can be considerable (Williams, 1988; Walker et al., 1989). Negative effects of escaped hydrocarbons from vessels range from large-scale mortality resulting from spills (Diaz-Piferrer, 1962; Nadeau and Berquist, 1977) to sublethal effects such as reduced carbon uptake by the grasses (McRoy and Williams, 1977). Vessels also impact seagrasses by trawling (Eleuterius, 1987) and shading by houseboats (pers. obs.). Other anthropogenous sources of impact include sedimentation resulting from dam construction, near-shore development, and borrow pits (Zieman, 1982; Livingston, 1987), pulp mill effluents (Hooks et al., 1976; Livingston, 1982; 1984), heated effluents from power plants (Roessler and Zieman, 1969; Zieman, 1970; Thorhaug et al., 1973), and increased epiphyte cover resulting from eutrophication (Sand-Jensen, 1977; 1989; Silberstein et al., 1986). When disturbance is severe enough to remove portions of the seagrass rhizome mat, "blowouts", or denuded areas of negative topography, result (e.g., Patriquin, 1975; González-Liboy, 1979; Wanless, 1981).

Forces which open gaps in seagrass canopies impact the associated

benthic fauna as well. The grassbed fauna is directly dependent upon the seagrass canopy; unvegetated sediment has very low epifaunal abundance relative to well-developed seagrass canopies (Orth et al., 1984; Summerson and Peterson, 1984; Wilson et al., 1990; Sogard and Able, 1991). Bare patches cause an edge effect and are used heavily as foraging areas by large mobile predators (Heck and Orth, 1980; Holt et al., 1983; Summerson and Peterson, 1984). Sparse seagrass also supports low numbers of fauna relative to dense seagrass (e.g., Holmquist et al., 1989b), in large part due to faunal preference (Bell and Westoby, 1986), and there appears to be a seagrass density threshold below which recruitment is low (Worthington et al., 1991) and susceptibility to predation is high (Nelson, 1979; Heck and Thoman, 1981).

Slow recovery after disturbance is typical for seagrasses (Wanless, 1969; Patriquin, 1975; Turner, 1985; Williams 1988; 1990; Clarke and Kirkman, 1989; Holmquist, 1992); small impacts such as propeller and anchor damage can have lasting effects (Zieman, 1976; González-Liboy, 1979). Slow recovery makes the transplanting of seagrasses for mitigation a relatively complex endeavor (Fonseca et al., 1985; 1987a; b; c; Lewis 1987). Most seagrasses, such as *Thalassia testudinum*, the dominant seagrass in the subtropical U.S. and Caribbean, are not well adapted for rapid recolonization, because of a slow rate of rhizome elongation, a low rate of population growth, few seeds, no seed reserve, poor seedling success, and low productivity (e.g., Williams, 1990). *Thalassia* only recolonizes gaps by perrenation (Williams, 1990), and recovery is particularly slow when rhizomes are damaged (Patriquin, 1975; Zieman, 1976), because an injured *Thalassia* meristem requires about one year for repair (Fuss and Kelly, 1969; Kelly et al., 1971).

Input of nutrients from coastal development and resuspended sediments may exacerbate initial anthropogenous disturbance to seagrasses and greatly protract the already lengthy recovery period for both naturally recovering and transplanted seagrasses. Disturbance to seagrasses and eutrophication tend to co-occur in developed coastal areas. Macroalgae are increasing in importance in many coastal waters because of their rapid response to nutrient influx (e.g., Shepherd et al., 1989; Lavery et al., 1991; Sand-Jensen and Borum, 1991); nuisance algae can proliferate to virtually cover areas on the scale of hectares (Virnstein and Carbonara, 1985) or occasionally square kilometers (Olafsson, 1988). Unattached algal masses, 10 to 50 cm in diameter, are benthic analogs of terrestrial tumbleweeds and can roll up to 0.5 km/day (Holmquist, 1994). These algae frequently settle in sheltered areas (Josselyn, 1977; Zieman et al., 1989) and may tumble into blowouts and remain entrapped by the wall of undisturbed shoots on the gap perimeters. Drift nuisance algae may be powerful vagile colonizers, and in many systems (e.g., Miller, 1982; Sousa, 1985), vagile colonizers are better able to exploit gaps than are vegetative colonizers. In seagrass-algal systems, drifting algal masses should be particularly formidable, because algal clumps arrive as large individuals immediately capable of competing instead of as small colonizing spores. Algae settling into gaps are likely to compete directly with vegetatively recolonizing seagrass for light and/or dissolved gasses. Shoots of aquatic grasses have high light compensation points and high light saturation levels (Sand-Jensen and Borum, 1991), and various experiments have shown shading to have negative effects on seagrasses (Dennison and Alberte, 1982; Bulthuis, 1983; Tomasko and Dawes, 1989). Algal masses which settle into gaps may intercept substantial amounts of light above recovering seagrass. Algal mats in other

systems can produce anoxic conditions (Olafsson, 1988; Everett, 1991; Lavery and McComb, 1991), and underlying, regenerating seagrasses could suffer from competition for dissolved oxygen.

The differential height of blades within and outside the patch will be highest immediately after initial disturbance, and algae may be most likely to be trapped at this time. Disturbance in the seagrass-drift algal system may result in long-term effects; not only is seagrass slow to recolonize space, but the probability of further disturbance via algal cover may be highest immediately after initial gap formation. Repeated removal of blades slows leaf regrowth and reduces below-ground biomass (references and discussion in Valentine and Heck, 1991). Re-colonization of canopy gaps resulting from human disturbance may be greatly slowed, or even fail to occur, if diffuse nutrient input and associated eutrophication has led to increased nuisance algal abundance in a given seagrass system. In turn, transplantation efforts in such a system could be significantly more difficult.

In addition, large-scale algal cover resulting from such a disturbance-eutrophication synergism could cause a shift in seagrass species composition with ensuing consequences for erosion control. For example, *Halodule wrightii*, a species of secondary importance, is inferior to *Thalassia* in terms of mitigation of sediment erosion (Fonseca and Fisher, 1986). Relative to *Thalassia*, *Halodule* generally has a faster rate of rhizome elongation, higher rate of population growth, relatively plentiful seeds, a better seed reserve, higher seedling success, and higher productivity (Williams, 1990). *Halodule wrightii* is generally viewed as a pioneering species and increases in abundance following disturbance, although *Halodule* also requires considerable time for recovery and does not

approach the biomass levels of *Thalassia* (Zieman, 1982; Williams, 1990; Holmquist, 1992). Because species which are good colonizers are favored in gaps (Miller, 1982), and because *Halodule* is a greatly superior colonizer relative to *Thalassia*, the former species could dominate disturbed patches for an extended time if recovery is slowed by the presence of nuisance algae.

Although it seems intuitive that recovery from small disturbances should be rapid and that recovery from large canopy gaps should be slow, the inverse relationship could hold when eutrophication is coupled with human disturbance. Large canopy gaps may "capture" rolling algal masses along one portion of the gap periphery, but accumulations could be limited by shifting currents. Conversely, small gaps the size of propeller and anchor scars may shelter accumulated algae from all directions, because of the tall flow shadow formed by the close and comparatively tall walls of seagrass around the gap perimeter. Algal disturbance following the initial impact could persist indefinitely in gaps resulting from small-scale impact.

Drift algal accumulations are poor "Band-Aids" for disturbed seagrass assemblages (Holmquist, 1992). Various fauna, particularly caridean and penaeid shrimp, are reduced in abundance in these algal accumulations (Holmquist, 1992). Caridean shrimps are important food items for many grassbed fishes (Zieman, 1982; Livingston, 1982; 1984) and are the dominant prey for juveniles of commercially important fishes (Rutherford et al., 1982; 1983; Hettler, 1989); penaeid shrimps are a major fishery resource. In addition, the habitat quality of drift algal mats may be further mitigated by ephemerality. Algal mats periodically break up or senesce, leaving behind bare sediment. Most importantly, the mats inhibit recovery of seagrass, i.e. the primary source of fauna. Abundant macroalgae and protracted recovery periods for impacted seagrass meadows should both

alter the functional biodiversity of the benthic assemblage and reduce output of recruits to populations of commercial species.

Objectives

The primary objectives of the project were 1) to determine if recovery following impact to seagrasses along waterways is slowed or otherwise altered by increased presence of nuisance macroalgae resulting from eutrophication, and 2) to determine the extent to which recovery rate is a function of size of initial impact. My null hypotheses were: 1) recovery of seagrass, and composition of the assemblage of seagrasses, will not differ between a) denuded seagrass plots from which algae are excluded and b) denuded plots which allow entry of algae, and 2) recovery rate will not vary across disturbed plots of differing sizes.

Study Site and Methods

I performed this work at La Parguera, in southwest Puerto Rico. Like many other coastal systems, the La Parguera area has attracted both widespread development and heavy boat traffic. Anchor and propeller scarring is common in the area (González-Liboy, 1979) as is sediment scour from vessels greater than 15 m in length (pers. obs.). There has recently been massive sediment input from housing developments and hillside borrow sites, and nutrient levels are high as a result of direct, untreated sewage input from shoreline dwellings. Unattached drift algae of the genus *Dictyota* are highly abundant, and cover the surface of most observed blowouts in the area's seagrass meadows (pers. obs.). The expansive grassbeds in this system are dominated by *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* (species in descending order of abundance; Vicente, 1975;

Villamil and Canals, 1981), and serve an important nursery function for local species (Kolehmainen, 1972; Villamil and Canals, 1981).

I used a series of manipulations designed to test the extent to which recovery of impacted seagrass is a function of 1) size of initial disturbance, and 2) increased presence of macroalgae due to eutrophication; null hypotheses are "no effect". This work involved a 2 X 3 factorial in blocks design, blocking for location ($n=12$; Fig. 1). Treatments and levels were as follows: Treatment 1= Size of disturbance, Levels: a) Large (1 square meter), and b) Small (0.25 square meters); Treatment 2= Algal presence, Levels: a) Unmanipulated Control plots of seagrass against which recovery can be gauged, b) Disturbed/Unfenced plots which allowed access to algae, and c) Disturbed/Fenced plots which exclude algae. The experiment thus involved a total of 72 plots. More rapid recovery on the Disturbed/Fenced plots would suggest that the ambient drift algal population interfered with the recovery process.

I randomly selected twelve stations, and in turn randomly selected six plots at each station. Each of the six plots was allocated to one of the six levels included in the experiment; I thus blocked for location. Prior to the experiment, the field team a) counted all short shoots of all seagrass species, b) counted all green algal holdfasts, c) measured the longest blade of each short shoot within 1) each of the 36 0.25 square meter plots, and 2) four randomly-placed 0.25 square meter quadrats in each of the 36 one square meter plots. Lastly, I subsampled seagrass growth form by collecting all short shoots and green algae within randomly-placed 15 cm² quadrats (one quadrat in each 0.25 square meter plot, two in each one square meter plot). Short shoots were gathered by hand and transported on ice to the laboratory where the seagrass shoots of each species were counted and

measured. These measures included number of short shoots per quadrat, blade length and width, and number of blades per shoot. I used these characteristics to calculate the growth form parameters of shoot density, canopy height, blade density, and leaf area index as per the methods of Sogard et al. (1987) and Holmquist et al. (1989b). The photosynthetic portion of all seagrass blades collected within each quadrat was washed in dilute HCl to remove carbonate epiphytes and sediment and then dried at 95°C for 24 h to determine g dry mass of the standing crop for each sample. The seagrass growth form parameters, standing crop, and total seagrass cover were the dependent variables in the study.

After initial sampling, I used modified shovels to remove seagrass on experimental plots to a depth of 10 cm in order to simulate damage caused by anchor or propeller scarring; the removed material included a significant portion of the rhizome layer. Plastic fencing, consisting of 30 cm-tall walls of 2.5 by 5 cm mesh, was established 5 meters upcurrent of the algal exclusion plots to block ingress of tumbling algae (Fig. 1). The two denuded control groups and the unmanipulated controls were not be fenced. The fencing was supported by PVC stakes and had a 10 cm gap between the substrate and bottom.

Plots were then surveyed weekly to determine the extent of algal cover and to remove epiphytes from fencing. We also removed any fence-hopping algae from the algal exclusion plots on a weekly basis. Although some algae did bypass the fencing and accumulate on the exclusion plots, amounts were relatively minimal (see below) and algae were never allowed to persist on these plots for more than seven days before removal. Seagrass was censused, as described above, at 2 mo intervals.

Summary of most important results

Data

The experimental treatments caused severe and long-lasting effects on seagrasses on our plots (Figs. 2-6; Tables 1-5). After fourteen months of recovery (at which time the algal barriers were removed), percent seagrass cover, *Thalassia* shoots, standing crop, and leaf area index were all still significantly lower on the two types of disturbed plots (with and without further algal disturbance) than on the controls; canopy height was the sole exception. This difference was maintained despite a trend of overall reduction of *Thalassia* during the study period, probably due to bedload transport of sand onto several stations. The disturbed plots remained more depauperate than the controls twenty months after initial disturbance.

Algal cover was much higher on disturbed/algal access plots than on controls, and these significant differences persisted for at least twenty months (Fig. 7; Table 6). Mean algal cover on the disturbed/algal access plots was initially high (58%) but the level of cover fell steadily in conjunction with seagrass recovery. Within these experimental plots, there was significantly higher algal cover initially associated with small disturbances (mean= 79%) than with large disturbances (38%; Fig. 8). These differences ceased after about a year of recovery.

Percent seagrass cover and *Thalassia* shoots were lower on disturbed/algal access plots than on disturbed/algal exclusion plots throughout most of the study (Figs. 2-3; Tables 1-2). These two classes of manipulated plots did not demonstrate consistent significant differences for standing crop, leaf area index, or canopy height (Figs. 4-6; Tables 3-5). Recovery, as measured by the entire suite of response variables (exclusive of canopy height), was slower on the disturbed/algal access plots than on

disturbed/algal exclusion plots (mean for Kendall's coefficient of concordance = 0.813, $p = 0.039$). We were able to contrast recovery as a function of disturbance size for two parameters: percent seagrass cover and *Thalassia* shoots. There were no differences as a function of disturbance size for seagrass cover (Fig. 9), but there was a higher density of *Thalassia* shoots associated with the small disturbances than with the larger disturbances at the end of the project (Fig. 10).

Significance

It is clear that rhizome-level damage, such as that produced by anchor and propeller scarring, causes a long-term impact on seagrass meadows. The experimental plots have not recovered from these relatively small scale disturbances, and I expect that an additional three years will be required before recovery is complete. I intend to continue monitoring the plots on a bi-yearly basis until recovery is complete.

As hypothesized, disturbed plots accumulated more drift algae than controls because of the negative topography resulting from rhizome and canopy removal. Further, small plots garnered more algae than large plots; the results provide a strong indication that this additional algal accumulation is due to the small gap area : canopy height ratio present in the small gaps, i.e., once entrained, algal clumps are unlikely to be rolled out of a small gap because the closely-set canopy walls shield clumps from the ambient water flow. Thus, in this system, additional disturbance forces (algal accumulations) are brought to bear on recently disturbed patches, and the extent of this positive feedback is inversely related to the spatial scale of initial disturbance. Both of these phenomena diminish with continued recovery of a gap. The seagrass-algal system therefore demonstrates an

exception to the shifting mosaic model (i.e., recently-disturbed patches *least* likely to be disturbed following an initial disturbance). If the shifting mosaic model obtained in the seagrass-algal milieu, we would expect increasing intensity of disturbance to accompany recovery rather than the observed inverse relationship.

Algal accumulations represented a disturbance force that reduced percent cover and density of *Thalassia* shoots on plots from which drift algae were not excluded. Standing crop and leaf area index were not affected, suggesting that there may have been a degree of compensatory response in which the reduced number of shoots on the disturbed plots produced somewhat larger blades. A greater intensity of disturbance fell upon the smaller plots, but recovery on these gaps was equal to or greater than exhibited by the large gaps, probably due to the small amount of perennation required to seal small gaps. Although algal accumulations did slow recovery on algal access plots relative to algal exclusion plots, these effects are likely to be greater in other seagrass systems. Our study area was a relatively high energy back-reef system in which the sediment had reduced fines and low organic content; these characteristics are associated with reduced canopy height (Holmquist et al., 1989 a; b). The canopy heights on our sites were in fact low (about 100 mm) for subtidal seagrasses. It is likely that algal retention would have been more pronounced, and seagrass recovery further slowed, in systems with taller canopies.

Presence of nutrient-limited macroalgae is clearly an important determinant of seagrass recovery. Large ambient populations of nuisance macroalgae can slow recovery of anthropogenously-disturbed SAV along waterways. Relatively minor propeller and anchor damage will likely have longer-lasting effects if recovery of seagrasses is protracted by

eutrophication. The results emphasize the importance of minimizing boating activity in shallow water immediately adjacent to waterways, perhaps by marking shallow grassbeds near channels as being off-limits to power boats. Further, this work should assist with the development of timetables for predicting recovery of seagrass-dominated assemblages from disturbance both in the presence and absence of eutrophication or large nuisance algal populations; longer recovery periods and continued resuspension of sediments near channels should probably be anticipated in eutrophic areas. Information on initial impact and ensuing recovery times provided by this study should be of use in estimating economic costs associated with anthropogenous disturbance of seagrasses and in making decisions concerning seagrass transplantation as part of mitigation programs (e.g., an ideal mitigation site might be best placed in an area without exogenous nutrient input or a large macroalgal population).

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Bibliography

- Bell, J. D., and M. Westoby. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* **68**: 205-209.
- Bulthuis, D. A. 1983. Effects of *in situ* light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *J. Exp. Mar. Biol. Ecol.* **53**: 193-207.
- Bulthuis, D. A., G. W. Brand, and M. L. Mobley. 1984. Suspended sediments and nutrients in water ebbing from seagrass-covered and denuded tidal mudflats in a southern Australian embayment. *Aquat. Bot.* **20**: 257-266.
- Clarke, S. M., and H. Kirkman. 1989. Seagrass dynamics. Pages 304-345 in A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, editors. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, The Netherlands.
- Delgado Hyland, A. 1991. Las praderas de *Thalassia*. Boletín Oficial, Reserva Natural Bahía de Jobos **11**: No. 6.
- Dennison, W. C., and R. S. Alberte. 1982. Photosynthetic responses of *Zostera marina* L. (eelgrass) to *in situ* manipulations of light intensity. *Oecologia* **55**: 137-144.
- Diaz-Piferrer, M. 1962. Las algas superiores y fanerogamas marinas. Pages 273-307 in *Ecología marina*. Fundación la Salle de ciencias naturales. Caracas, Venezuela.
- Eleuterius, L. N. 1987. Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi. Pages 11-24 in M. J. Durako, R. C. Phillips, and R. R. Lewis, III, editors. *Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States*. Florida Dept. of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida, USA.
- Everett, R. A. 1991. Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. *J. Exp. Mar. Biol. Ecol.* **150**: 223-247.
- Fonseca, M. S. 1989. Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. *Estuar. Coast. Shelf Sci.* **29**: 501-507.

Fonseca, M. S., and J. A. Calahan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuar. Coast. Shelf Sci.* **35**: 565-576.

Fonseca, M. S., J. S. Fisher, J. C. Zieman, and G. W. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuar. Coast. Shelf Sci.* **15**: 351-164.

Fonseca, M. S., W. J. Kenworthy, G. W. Thayer, D. Y. Heller, and K. M. Cheap. 1985. Transplanting of the seagrasses *Zostera marina* and *Halodule wrightii* for sediment stabilization and habitat development on the east coast of the United States. Technical Report EL-85-9, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Fonseca, M. S., W. J. Kenworthy, K. Rittmaster, and G. W. Thayer. 1987a. The use of fertilizer to enhance transplants of the seagrasses *Zostera marina* and *Halodule wrightii*. Technical Report EL-87-12, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Fonseca, M. S., W. J. Kenworthy, and G. W. Thayer. 1987b. Transplanting of the seagrasses *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum* for sediment stabilization and habitat development in the southeast region of the United States. Technical Report EL-87-8, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Fonseca, M. S., G. W. Thayer, and W. J. Kenworthy. 1987c. The use of ecological data in the implementation and management of seagrass restorations. Pages 175-188 in M. J. Durako, R. C. Phillips, and R. R. Lewis, III, editors. *Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States*. Florida Dept. of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida, USA.

Fonseca, M. S., J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in structuring seagrass meadows. *Estuar. Coast. Shelf Sci.* **17**: 367-380.

Fuss, C. M., and J. A. Kelly. 1969. Survival and growth of sea grasses transplanted under artificial conditions. *Bull. Mar. Sci.* **19**: 351-365.

Godcharles, M. F. 1971. A study of the effects of a clam dredge on benthic communities in estuarine areas. Tech. Ser. 64, Dep. of Res. Lab. F.D.N.R., Div. of Mar. Res., St. Petersburg, Florida, USA.

- González-Liboy, J. 1979. An examination of the present condition of seagrass meadows in La Parguera, Puerto Rico. Dept. Natural Resources Final Report to Dingell-Johnson Project F-4, U. S. Fish and Wildlife Service.
- Grigg, D. I., E. L. Shatrosky, and R. P. Van Eepoel. 1971. Operating efficiencies of package sewage plants on St. Thomas, V. I., August-December, 1970. Caribb. Res. Inst. Water Pollut. Rep. 12.
- Harlin, M. M., B. Thorne-Miller, and J. C. Boothroyd. 1982. Seagrass-sediment dynamics of a flood-tidal delta in Rhode Island (USA). *Aquat. Bot.* 14: 127-138.
- Heck, K. L., Jr., and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 in V. S. Kennedy, editor. *Estuarine perspectives*. Academic Press, New York, New York, USA.
- Heck, K. L., Jr., and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53: 125-134.
- Hettler, W. F., Jr. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bull. Mar. Sci.* 44: 155-162.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6: 65-70.
- Holmquist, J. G. 1992. Disturbance, dispersal, and patch insularity in a marine benthic assemblage: influence of a mobile habitat on seagrasses and associated fauna. Dissertation. Florida State University, Tallahassee, FL.
- _____. 1994. Benthic macroalgae as an alternative dispersal mechanism for fauna: influence of a marine tumbleweed. *J. Exp. Mar. Biol. Ecol.* 180: 235-251.
- Holmquist, J. G., G. V. N. Powell, and S. M. Sogard. 1989a. Decapod and stomatopod communities of seagrass-covered mud banks in Florida Bay: inter- and intra-bank heterogeneity with special reference to isolated subenvironments. *Bull. Mar. Sci.* 44: 251-262.

- _____. 1989b. Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. *Mar. Biol.* **100**: 473-483.
- Holt, S. A., C. L. Kitting, and C. R. Arnold. 1983. Distribution of young red drums among different seagrass meadows. *Trans. Am. Fish. Soc.* **112**: 267-271.
- Hooks, T. A., K. L. Heck, Jr., and R. J. Livingston. 1976. An inshore marine invertebrate community: structure and habitat associations in the northeastern Gulf of Mexico. *Bull. Mar. Sci.* **26**: 99-109.
- Josselyn, M. N. 1977. Seasonal changes in the distribution and growth of *Laurencia poitei* (Rhodophyceae, Ceramiales) in a subtropical lagoon. *Aquat. Bot.* **3**: 217-229.
- Kelly, J. A., C. M. Fuss, and J. R. Hall. 1971. The transplanting and survival of turtle grass, *Thalassia testudinum*, in Boca Ciega Bay, Florida. *Fisheries Bulletin* **69**: 273-280.
- Kenworthy, W. J., and D. Haunert. 1991. The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. NOAA Technical Memorandum NMFS-SEFC-287, 181 pp.
- Kolehmainen, S. E. 1972. Ecology of turtle grass (*Thalassia testudinum*) beds in Jobos Bay. Aguirre Power Project Environmental Studies Annual Report (PRNC-162), Puerto Rico Nuclear Center.
- Lavery, P. S., R. J. Lukatelich, and McComb. A. J. 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. *Estuarine Coastal Shelf Sci.* **33**: 1-22.
- Lavery, P. S., and A. J. McComb. 1991. Macroalgal-sediment nutrient interactions and their importance to macroalgal nutrition in a eutrophic estuary. *Estuarine Coastal Shelf Sci.* **32**: 281-295.
- Leber, K. M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology* **66**: 1951-1964.
- Levy, D. 1992. Puerto Rico exports Hispanic scientists. *Science* **258**: 1191.

- Lewis, F. G., III, and A. W. Stoner. 1983. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. *Bull. Mar. Sci.* **33**: 296-304.
- Lewis, R. R., III. 1987. The restoration and creation of seagrass meadows in the southeastern United States. Pages 153-174 *in* M. J. Durako, R. C. Phillips, and R. R. Lewis, III, editors. *Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States*. Florida Dept. of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida, USA.
- Livingston, R. J. 1982. Trophic organization of fishes in a coastal seagrass system. *Mar. Ecol. Prog. Ser.* **7**: 1-12.
- _____. 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* **65**: 1258-1275.
- _____. 1987. Historic trends of human impacts on seagrass meadows in Florida. Pages 139-151 *in* M. J. Durako, R. C. Phillips, and R. R. Lewis, III, editors. *Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States*. Florida Dept. of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida, USA.
- McRoy, C. P., and S. L. Williams. 1977. Sublethal effects of hydrocarbons on seagrass photosynthesis. Final Rep. to NOAA. Outer Continental Shelf Environmental Assessment Program Contract 03-5-022-56. 35pp.
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *Am. Nat.* **120**: 533-536.
- Nadeau, R. J., and E. T. Berquist. 1977. Effects of the March 18, 1973 oil spill near Cabo Rojo, Puerto Rico on tropical marine communities. Pages 535-538 *in* *Proceedings of the 1977 Oil Spill Conference*, New Orleans, LA. American Petroleum Institute, Washington, D.C.
- Nelson, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.* **38**: 225-245.
- Odum, H. T. 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intracoastal channel. *Publ. Inst. Mar. Sci. Tex.* **9**: 48-58.

- Olafsson, E. B. 1988. Inhibition of larval settlement to a soft bottom benthic community by drifting algal mats: an experimental test. *Mar. Biol.* **97**: 571-574.
- Orth, R. J., K. L. Heck, Jr., and J. v. Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* **7**: 339-350.
- Patriquin, D. G. 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. *Aquat. Bot.* **1**: 163-189.
- Pérès, J. M. 1984. La regression des herbiers à *Posidonia oceanica*. Pages 445-454 in C. F. Boudouresque, A. Jeudy de Grissac, and J. Olivier, editors. International workshop *Posidonia oceanica* beds. GIS Posidonie, Marseilles, France.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223-225.
- Roessler, M. A., and J. C. Zieman, Jr. 1969. The effects of thermal additions on the biota of Southern Biscayne Bay, Florida. Pages 136-145 in Proceedings of the Gulf and Caribbean Fisheries Institute 22nd Annual Session. Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- Rutherford, E. S., E. B. Thue, and D. G. Buker. 1982. Population characteristics, food habits and spawning activity of spotted seatrout, *Cynoscion nebulosus*, in Everglades National Park, Florida. Report T-668, U. S. National Park Service, South Florida Research Center, Homestead, Florida, USA.
- _____. 1983. Population structure, food habits, and spawning activity of gray snapper, *Lutjanus griseus*, in Everglades National Park. Report SFRC-83/02, U. S. National Park Service, South Florida Research Center, Homestead, Florida, USA.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* **3**: 55-63.
- _____. 1989. Environmental variables and their effect on photosynthesis of aquatic plant communities. *Aquat. Bot.* **34**: 5-25.

- Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquat. Bot.* **41**: 137-175.
- Shepherd, S. A., A. J. McComb, D. A. Bulthuis, V. Neverauskas, D. A. Steffensen, and R. West. 1989. Decline of seagrasses. Pages 346-393 *in* A. W. D. Larkum, A. J. McComb, and S. A. Shepherd, editors. *Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region*. Elsevier, Amsterdam, The Netherlands.
- Silberstein, K., A. W. Chiffings, and A. J. McComb. 1986. The loss of seagrass in Cockburn Sound, Western Australia. III. The effects of epiphytes on productivity of *Posidonia australis* Hook. f. *Aquat. Bot.* **24**: 355-371.
- Sogard, S. M., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine Coastal Shelf Sci.* **33**: 501-519.
- Sogard, S. M., G. V. N. Powell, and J. G. Holmquist. 1987. Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover. *Mar. Ecol. Prog. Ser.* **40**: 25-39.
- _____. 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bull. Mar. Sci.* **44**: 179-199.
- Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101-124 *in* S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego, California, USA.
- Summerson, H. C., and C. H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* **15**: 63-77.
- Taylor, J. L., and C. H. Saloman. 1968. Some effects of hydraulic dredging and coastal development in Boca Ciega Bay, Florida. *U.S. Fish Wildl. Serv. Fish. Bull.* **67**: 213-241.
- Thorhaug, A., D. Segar, and M. A. Roessler. 1973. Impact of a power plant on a subtropical estuarine environment. *Mar. Poll. Bull.* **4**: 166-169.

- Tomasko, D. A., and C. J. Dawes. 1989. Evidence for physiological integration between shaded and unshaded short shoots of *Thalassia testudinum*. Mar. Ecol. Prog. Ser. **54**: 299-305.
- Turner, T. 1985. Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. Ecology **66**: 83-92.
- Van Eepoel, R. P., and D. I. Grigg. 1970. Survey of the ecology and water quality of Lindberg Bay, St. Thomas. Caribb. Res. Inst. Water Pollut. Rep. 4. 6 pp.
- Valentine, J. F., and K. L. Heck, Jr. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. **154**: 215-230.
- Vicente, V. P. 1975. Sea grass bed communities of Jobos Bay. PRNC Report No. 196.
- Villamil, J., and M. Canals. 1981. Suplemento tecnico para el plan de manejo del area de Bahia de Jobos. Departamento de Recursos Naturales, San Juan, PR.
- Virnstein, R. W., and P. A. Carbonara. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. Aquat. Bot. **23**: 67-82.
- Walker, D. I., R. J. Lukatelich, G. Bastyan, and A. J. McComb. 1989. Effect of boat moorings on seagrass beds near Perth, Western Australia. Aquat. Bot. **36**: 69-77.
- Wanless, H. R. 1969. Sediments of Biscayne Bay - distribution and depositional history. Technical Report 69-2, Institute of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.
- _____. 1981. Fining-upwards sedimentary sequences generated in seagrass beds. J. Sediment. Petrol. **51**: 445-454.
- Ward, L. G., W. M. Kemp, and W. R. Boynton. 1984. The influence of waves and seagrass communities on suspended particles in an estuarine embayment. Mar. Geol. **59**: 85-103.

Williams, S. L. 1988. Disturbance and recovery of a deep-water Caribbean seagrass bed. *Mar. Ecol. Prog. Ser.* **42**: 63-71.

_____. 1990. Experimental studies of Caribbean seagrass bed development. *Ecol. Monogr.* **60**: 449-469.

Wilson, K. A., K. W. Able, and K. L. Heck, Jr. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Mar. Ecol. Prog. Ser.* **58**: 243-251.

Worthington, D. G., M. Westoby, and J. D. Bell. 1991. Fish larvae settling in seagrass: effects of leaf density and an epiphytic alga. *Aust. J. Ecol.* **16**: 289-293.

Zieman, J. C. 1970. The effects of a thermal effluent stress on the seagrasses and macroalgae in the vicinity of Turkey Point, Biscayne Bay, Florida. Ph.D. Dissertation. University of Miami, Coral Gables, Florida, USA.

_____. 1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. Pages 541-562 in L. E. Cronin, editor. *Estuarine research*. vol. 1. Academic Press, New York, USA.

_____. 1976. The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. *Aquat. Bot.* **2**: 127-139.

_____. 1982. The ecology of the seagrasses of south Florida: a community profile. Publication FWS/OBS-82/25, U. S. Fish and Wildlife Services, Office of Biological Services, Washington, D.C., USA.

Zieman, J. C., J. W. Fourqurean, and R. L. Iverson. 1989. The distribution and abundance of seagrasses in Florida Bay. *Bull. Mar. Sci.* **446**: 292-311.

Table 1. Percent seagrass cover as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 2 for means and standard errors.

Comparison	Before	8 Months	14 Months
Control v. Disturbed, algae excluded	0.16	$< 10^{-18}$ *	5.3×10^{-6} *
Control v. Disturbed, algal access	0.16	$< 10^{-18}$ *	1.7×10^{-8} *
Disturbed, algal access v. Disturbed, algae excluded	0.16	0.17	0.018 *

Table 2. *Thalassia* shoots as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 3 for means and standard errors.

Comparison	Before	8 Months	14 Months
Control v. Disturbed, algae excluded	0.10	3.5×10^{-9} *	6.7×10^{-7} *
Control v. Disturbed, algal access	0.036	5.0×10^{-9} *	8.0×10^{-9} *
Disturbed, algal access v. Disturbed, algae excluded	0.30	0.13	0.018 *

Table 3. Standing crop as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 4 for means and standard errors.

Comparison	Before	8 Months	14 Months
Control v. Disturbed, algae excluded	0.16	1.3×10^{-8} *	0.000037 *
Control v. Disturbed, algal access	0.013 *	7.0×10^{-9} *	0.000013 *
Disturbed, algal access v. Disturbed, algae excluded	0.12	0.31	0.17

Table 4. Leaf area index as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 5 for means and standard errors.

Comparison	Before	8 Months	14 Months
Control v. Disturbed, algae excluded	0.22	6.8×10^{-6} *	0.000034 *
Control v. Disturbed, algal access	0.25	3.2×10^{-6} *	6.5×10^{-6} *
Disturbed, algal access v. Disturbed, algae excluded	0.47	0.055	0.43

Table 5. Canopy height as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 6 for means and standard errors.

Comparison	Before	8 Months	14 Months
Control v. Disturbed, algae excluded	0.32	0.0053 *	0.060
Control v. Disturbed, algal access	0.47	0.00021 *	0.43
Disturbed, algal access v. Disturbed, algae excluded	0.32	0.13	0.097

Table 6. Percent algal cover as a function of algal access and time since disturbance: Per contrast p-values from multiple paired t-tests (one-way) for treatment effects at selected intervals since disturbance. * indicates significance at 0.05 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989). See Figure 6 for means and standard errors.

Comparison	1 Month	8 Months	14 Months
Control v. Disturbed, algae excluded	8.7×10^{-7} *	0.0030 *	0.042 *
Control v. Disturbed, algal access	$< 10^{-18}$ *	0.000057 *	0.0080 *
Disturbed, algal access v. Disturbed, algae excluded	$< 10^{-18}$ *	0.0018 *	0.0011 *

Figure legends

Figure 1. Schematic diagram of 2 X 3 factorial in blocks design. The design blocks for location; each of these treatment levels would be present at each of twelve stations (squares= disturbed plot boundaries, semi-circles= fencing, seagrass surrounds all plots). These treatments were established randomly at each station rather than as shown in the schematic. Disturbed plots (from which seagrass was removed) were of three sizes. For each size of disturbance, there was a) an undisturbed control plot of seagrass, b) a disturbed but unfenced plot which would allow access to algae, and c) a disturbed but fenced plot which would exclude algae. See text for further description.

Figure 2. Percent seagrass cover (means; error bars= standard errors) as a function of algal access and time since disturbance. A horizontal bar indicates that a given contrast was not significantly different at the 0.05 level (tests performed at the following intervals relative to disturbance: before, eight months after, and 14 months after). See Table 1 for precise per contrast and family-wise error rates.

Figure 3. *Thalassia* shoots/m² (means; error bars= standard errors) as a function of algal access and time since disturbance. A horizontal bar indicates that a given contrast was not significantly different at the 0.05 level (tests performed at the following intervals relative to disturbance: before, eight months after, and 14 months after). See Table 2 for precise per contrast and family-wise error rates.

Figure 4. Standing crop (grams dry mass/m²; means; error bars= standard errors) as a function of algal access and time since disturbance. A horizontal bar indicates that a given contrast was not significantly different at the 0.05 level (tests performed at the following intervals relative to disturbance: before, eight months after, and 14 months after). See Table 3 for precise per contrast and family-wise error rates.

Figure 5. Leaf area index (m²/m²; means; error bars= standard errors) as a function of algal access and time since disturbance. A horizontal bar indicates that a given contrast was not significantly different at the 0.05 level (tests performed at the following intervals relative to disturbance: before, eight months after, and 14 months after). See Table 4 for precise per contrast and family-wise error rates.

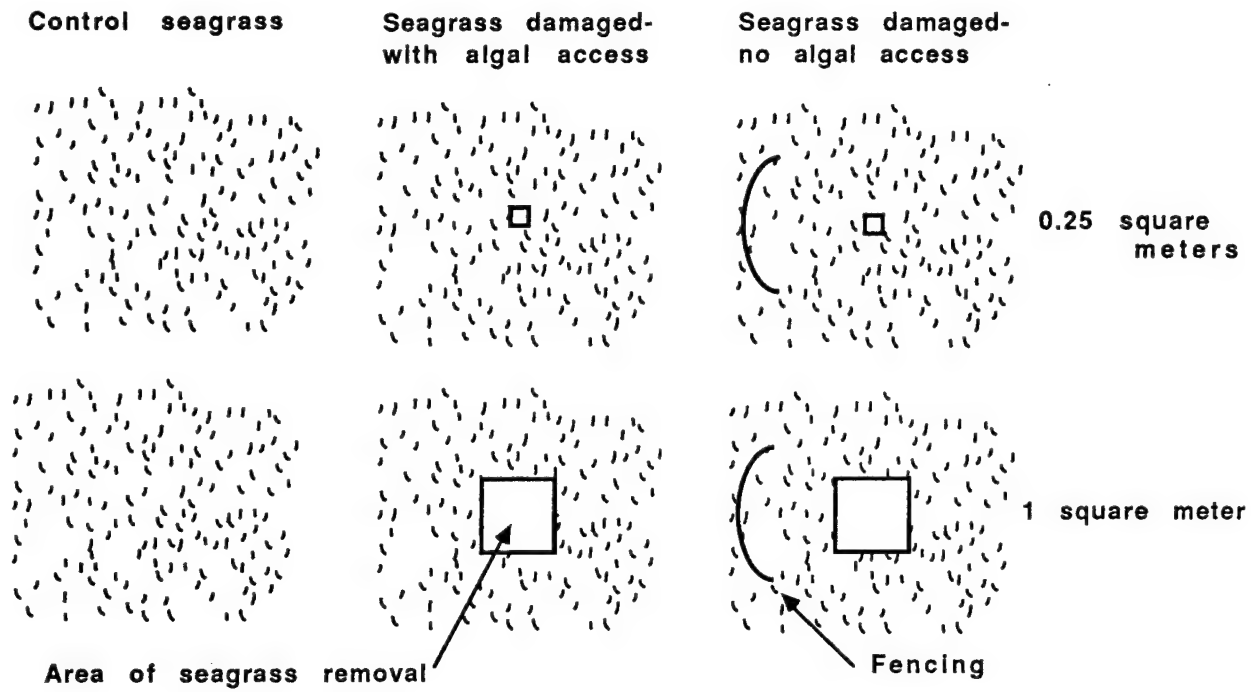
Figure 6. Canopy height (mm; means; error bars= standard errors) as a function of algal access and time since disturbance. A horizontal bar indicates that a given contrast was not significantly different at the 0.05 level (tests performed at the following intervals relative to disturbance: before, eight months after, and 14 months after). See Table 5 for precise per contrast and family-wise error rates.

Figure 7. Percent algal cover (means; error bars= standard errors) as a function of algal access and time since disturbance. See Table 6 for per contrast and family-wise error rates.

Figure 8. Percent algal cover (means; error bars= standard errors) as a function of size of initial gap size and time since disturbance. P-values represent results of paired t-tests (one-way) at selected intervals since disturbance. Contrasts for one and eight months were significant at the 0.032 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989).

Figure 9. Percent seagrass cover as a function of size of initial gap size and time since disturbance. P-values represent results of paired t-tests (one-way) at selected intervals since disturbance.

Figure 10. *Thalassia* shoots/m² as a function of size of initial gap size and time since disturbance. P-values represent results of paired t-tests (one-way) at selected intervals relative to disturbance. P-values represent results of paired t-tests (one-way) at selected intervals since disturbance. The contrast at fourteen months was significant at the 0.0012 level following conversion to family-wise error rates via sequential Bonferroni inequality (Holm, 1979; Rice, 1989).

**Fig. 1**

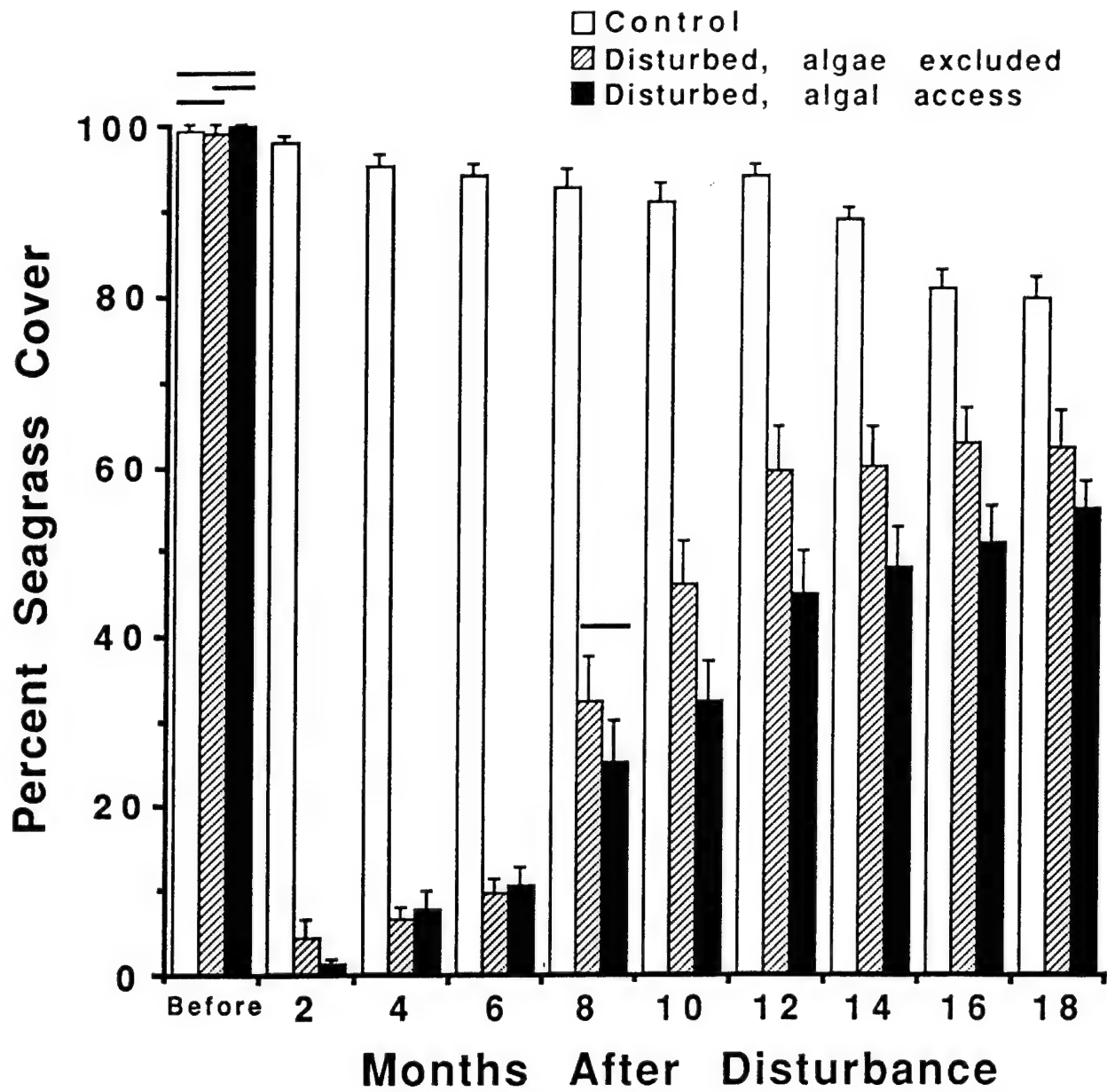


Fig. 2

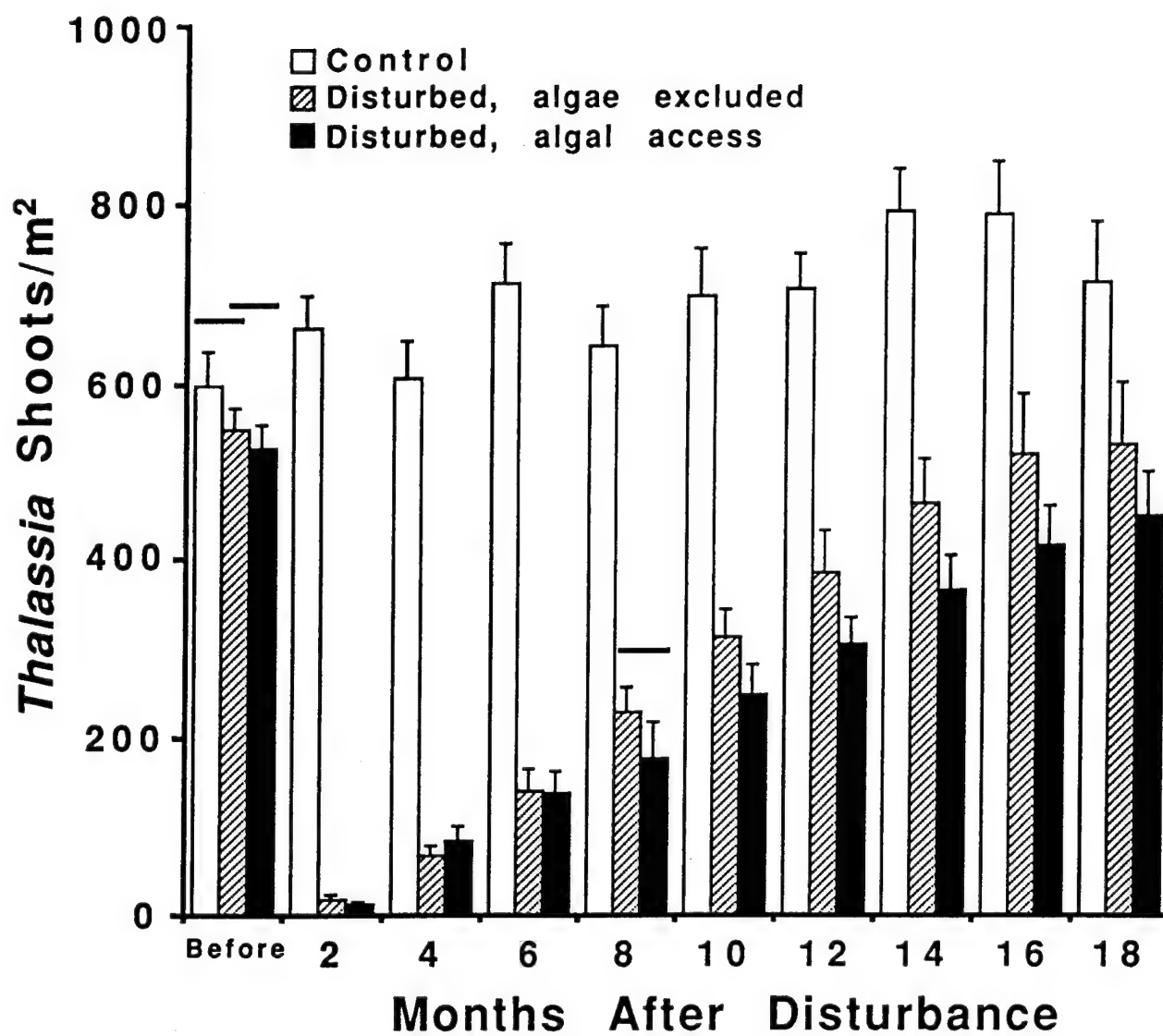


Fig. 3

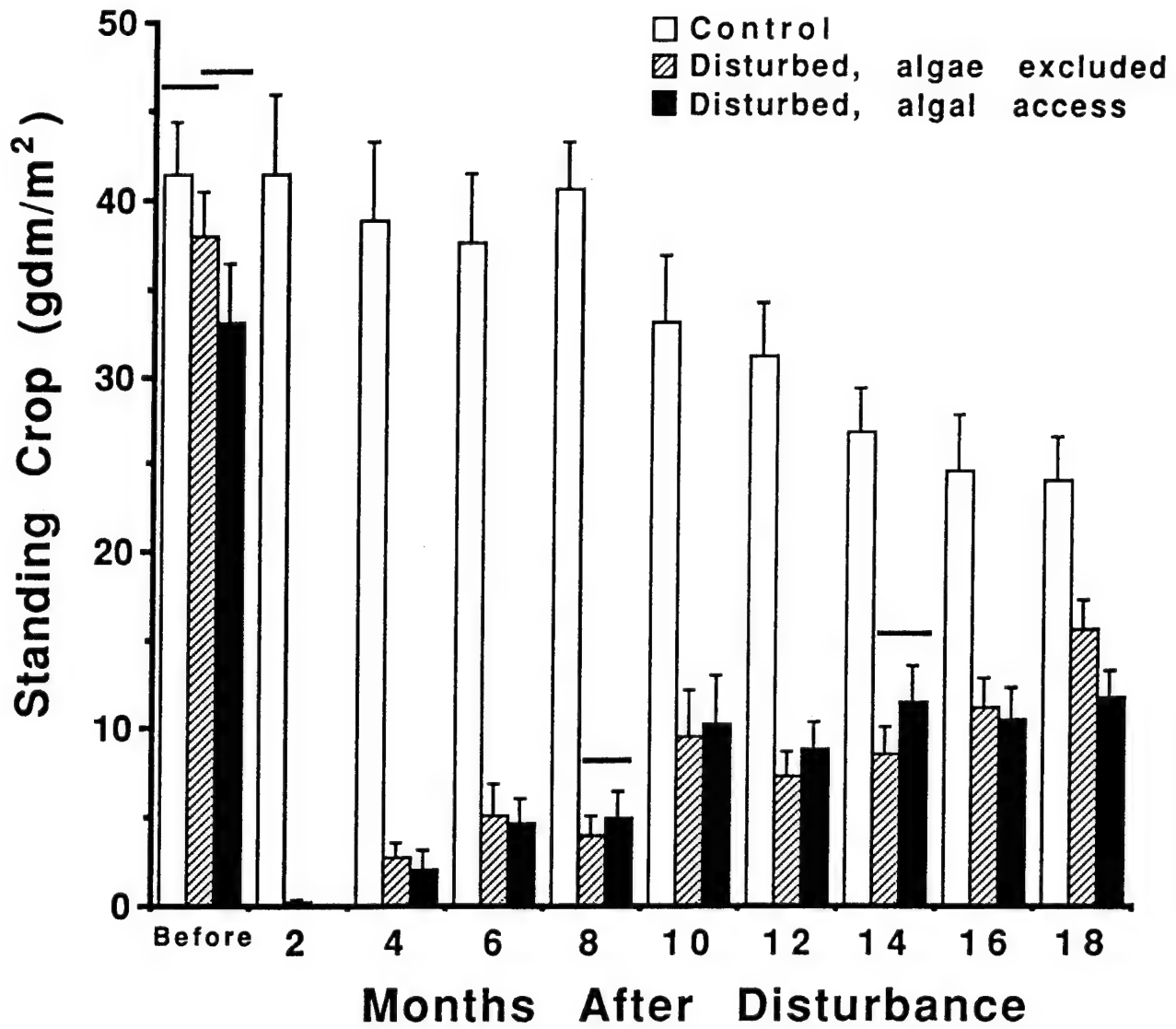


Fig. 4

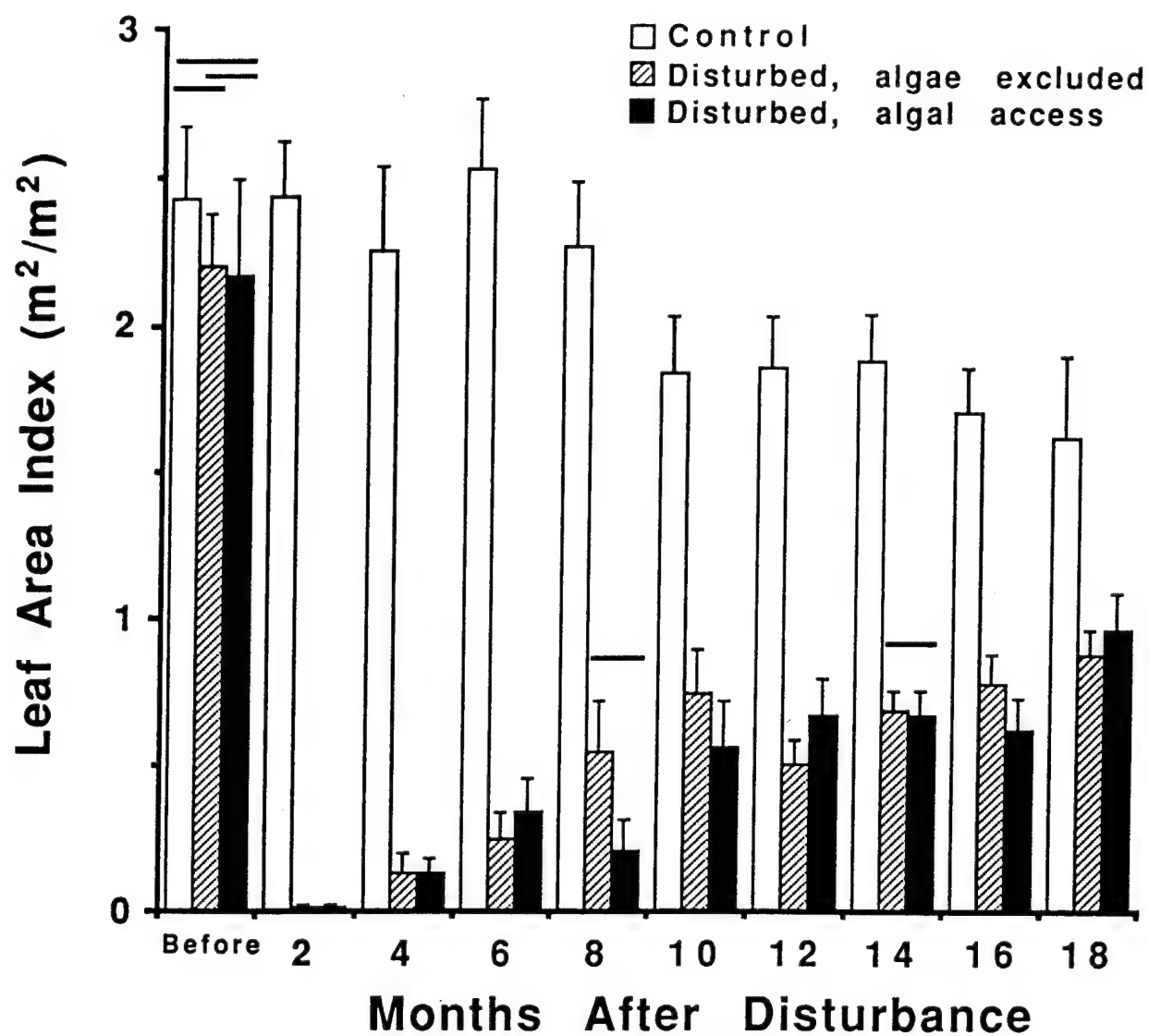


Fig. 5

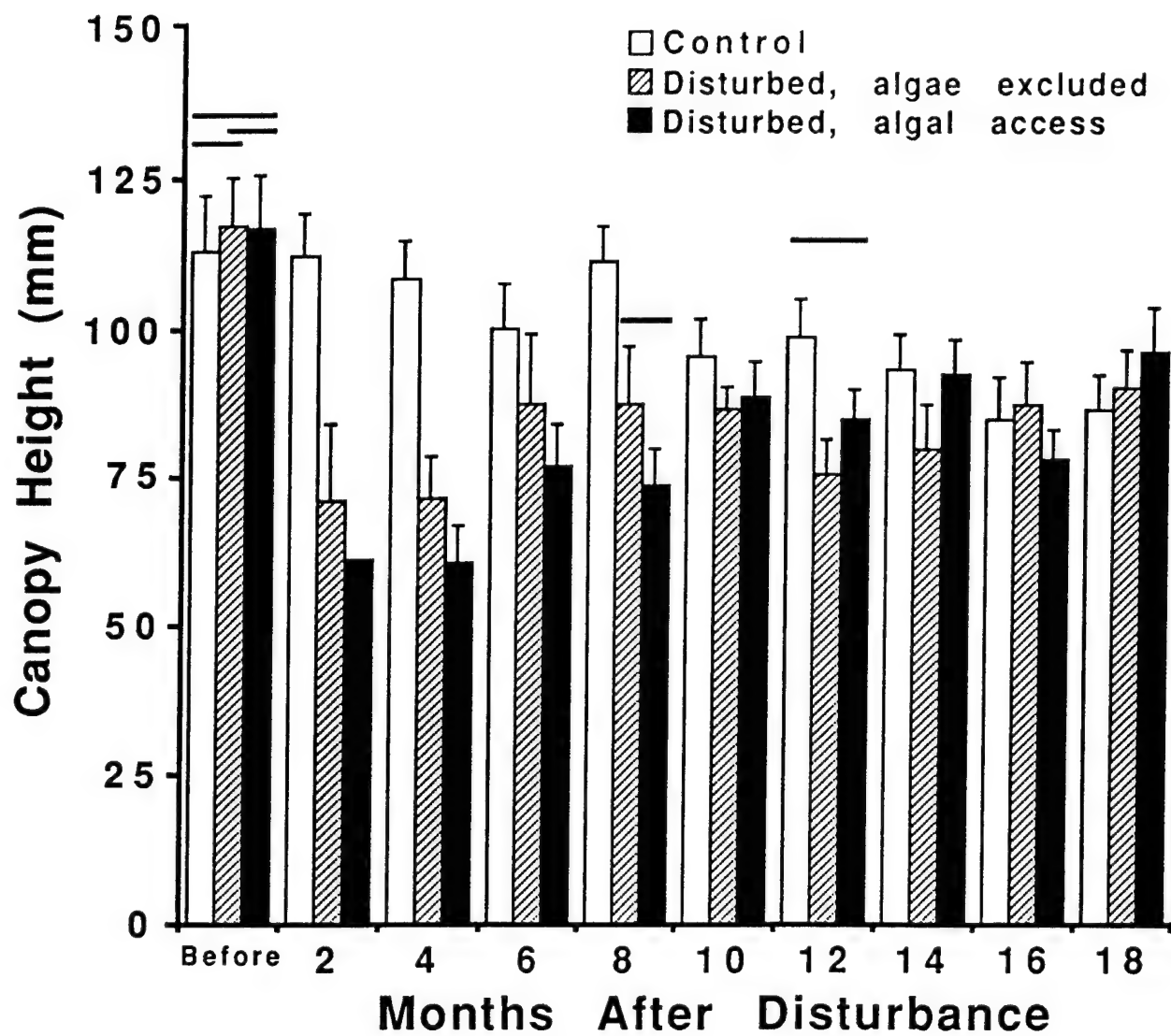


Fig. 6

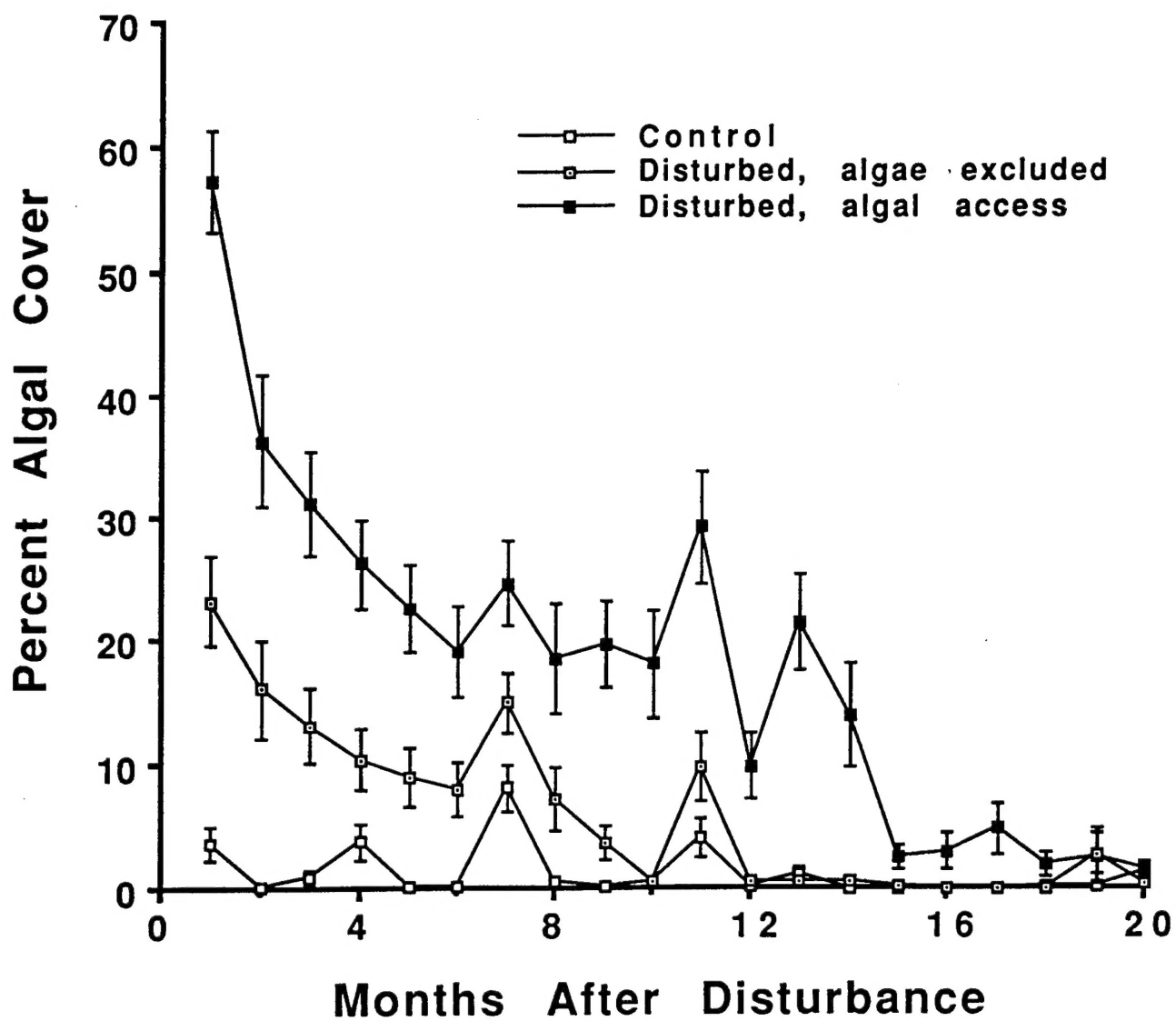


Fig. 7

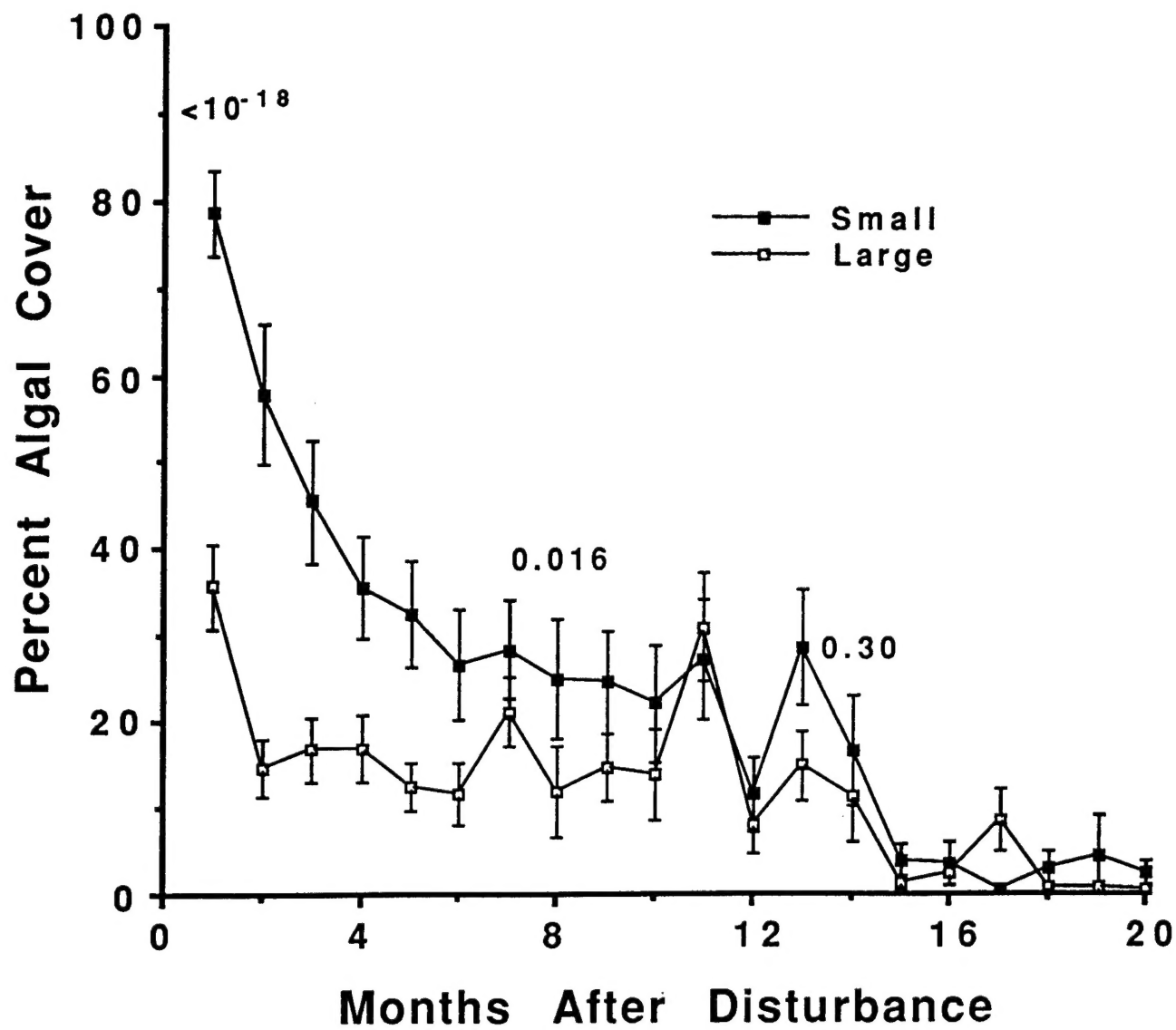


Fig. 8

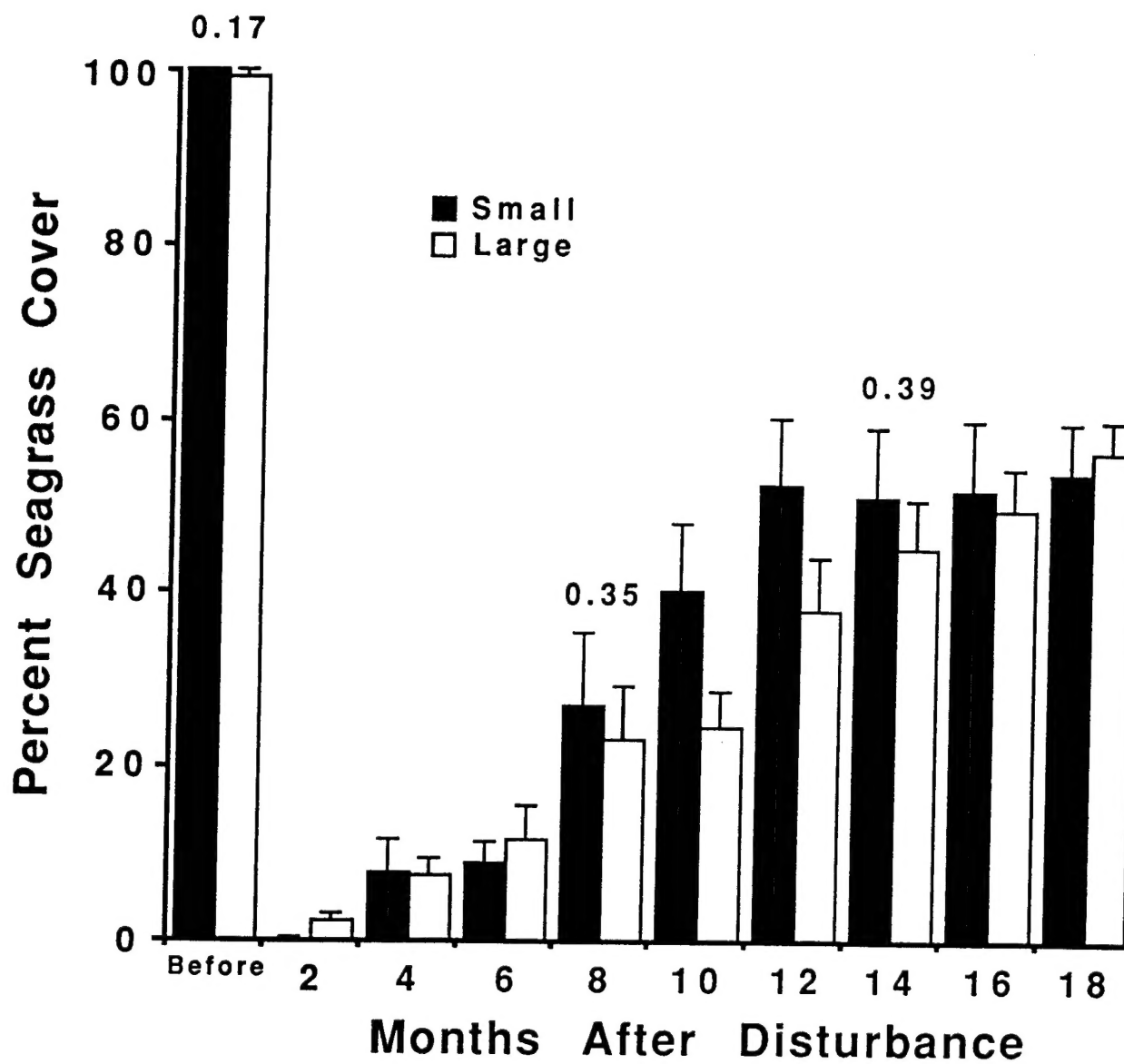


Fig. 9

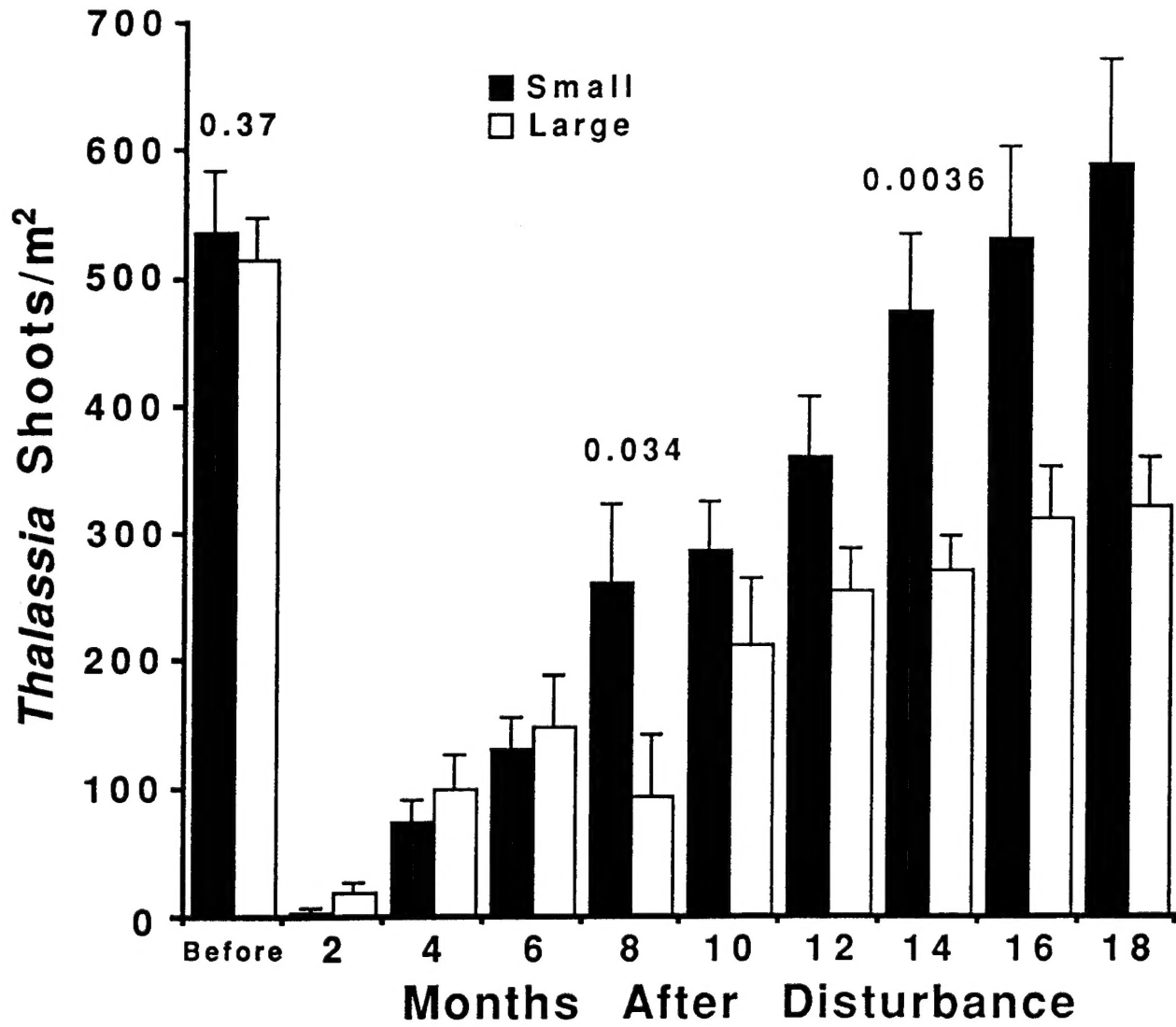


Fig. 10